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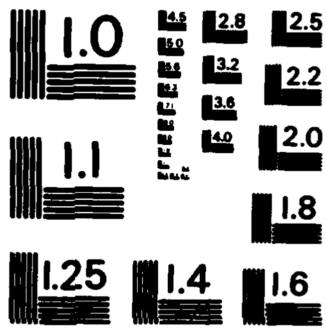

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VISUALLY EVOKED RESPONSES FROM NON-OCCIPITAL AREAS OF HUMAN CORTEX[*]

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ABSTRACT

Visually evoked neuromagnetic responses from the central area of the cerebral cortex in addition to the usual responses from the occipital areas of primary visual cortex were observed when the velocity of a moving grating pattern was modulated sinusoidally. The source of the central field has different functional properties than the source in primary sensory cortex. The position, depth, and orientation of the source are consistent with it lying in the Rolandic fissure near or in the eye representation area of motor cortex.

KEYWORDS

Neuromagnetism; magnetoencephalogram; visually evoked response; event-related responses

INTRODUCTION

It is now well established that many different areas of the brain respond to visual stimulation in various species of animals. These so-called extrastriate areas include the medial temporal (MT) region of the macaque monkey, and other areas as well, depending upon the species (Van Essen et al., 1981). Evidence exists that cells in some of these extrastriate areas are particularly responsive to moving patterns. We report visual experiments employing moving grating patterns that evoke magnetic fields whose distribution suggests the existence of similar extrastriate areas in humans.

METHODS

The stimuli were bar gratings created by a sinusoidal variation of the luminance across the screen of an oscilloscope. The speed of the grating was changed sinusoidally as it drifted, the modulation being expressed as a "velocity contrast" of 50%, giving the modulation amplitude as a percentage of the average velocity. Psychophysical thresholds for detecting a change in speed were obtained for this kind of stimulus by Kaufman and Williamson (1984). In the present neuromagnetic study the moving grating had a spatial frequency of 1.5 c/deg for one subject (SW) and 3 c/deg for another (PL). The average luminance was 49 cd/m^2, and the luminance contrast of the grating was nearly 100%. The gratings were caused to drift with an average speed of 3 or 5 deg/sec toward the left or the right of the subject. The frequency of modulation of the speed was 7 Hz. Thus when fixating at a black dot at the center of the screen, the subject saw a bar grating drifting in one direction and its speed changed from slow to relatively fast 7 times per second. This modulation frequency served as a reference signal for recovering responses through signal averaging with the steady-state paradigm.

The principles of neuromagnetic measurements are described in detail in a recent multi-authored text (Williamson et al., 1983). A SQUID sensor was used to measure the evoked field at various positions normal to the scalp. The detection coil was a second-order gradiometer of 2.4-cm diameter and 3.2-cm baseline separating adjacent coils. The output of the SQUID electronics was applied to a comb filter to reduce coherent noise at the power line frequency and then to a bandpass filter with 48 db/octave rolloff on either side of 7 Hz. The output of the filter was sent to a signal averager, and the phase lag and amplitude of each response, after one minute of averaging, were recorded.

Measurement positions are indicated by spherical coordinates θ,ρ of a reference system whose origin was judged to give the best constant-radius fit to the posterior half of the head. The corresponding Cartesian system has the +X-axis pointing posteriorly, +Y-axis toward the right shoulder, and +Z-axis upward. Plots shown in this paper present the axes in units of the radius R of the head, where R = 10 cm. The angle θ of a position is measured from the Z-axis, and the angle ρ from the +X-axis in a Z-plane. The orientation of a tangential vector, representing a current dipole model source, is indicated by the angle ψ by which its head is rotated counterclockwise from a plane of constant ρ, with $\psi = 0$ indicating that the dipole lies in the plane and points toward smaller values of θ.

RESULTS

The right hemispheres of two subjects (SW and PL) were studied in detail with two or more measurements at about 65 positions for each. Responses were observed over a wide area of the scalp from the occipital pole anteriorly to the central region. By studying how these responses varied with stimulus conditions it was possible to differentiate between activity associated with primary striate cortex in the visual area and éxtra-striate cortex in the more anterior areas. We shall describe the results on SW in detail; the essential features reported here are also seen in the data of the second subject PL.

Occipital Sources

Strong responses observed over the occipital area can be associated with sources in the primary sensory areas of the left and right hemispheres. Figure 1a is a view of the head seen from the back, with positions projected onto the Y-Z plane. Responses are denoted by phasers centered at the various measuring positions. Using data for responses to left and right visual field stimuli, the corresponding current dipoles in the right (RO) and left (LO) occipital regions were estimated by fitting their field patterns to the observed data. These patterns were calculated from the formulas given by Williamson and Kaufman (1981), including the corrections for finite diameter and baseline of the detection coil. Agreement is obtained with one dipole on each side of the midline, with approximately horizontal, opposing orientations. For simplicity we imposed the constraint that they have equal stength, depths and phase lags, and we adjusted the orientation of the LO source slightly so that the upper domain of its field pattern largely cancels the upper domain of the RO source, as is implied by the data in Fig. 1a for a full visual field presentation.

Figure 1b shows the phasers for the RO source, and Fig. 1c the phasers for the superimposed RO and LO souces. The dipole positions and other parameters are given in Table 1. Generally good agreement is achieved with the data in Fig. 1a. The one outstanding exception is the position Y/R=0.35, Z/R=-0.24, where the predicted field is more than twice the observed. This we believe is due to variability in the observed responses, since the data in Fig. 1a show the response at this position to be weaker than responses at positions to either side. Agreement is also less satisfactory in the area above this domain, where the upper domains of RO and LO (of opposite field direction) overlap. The anomalous phases observed here may well come from activity of another source in the right occipital area. Evidence of this was earlier found by Brenner et al. (1981) in the region between upper and lower domains of a source responding to contrast-reversal visual stimuli.

Central Source

The calculated field strength of the superimposed LO and RO field patterns is predicted to be barely detectable in the central area. In Fig. 2a are shown the measured responses in the parietal, temporal, and central areas, this time with positions projected onto the X-Z plane. In Fig. 2b are shown the observed responses with the predicted fields from LO and RO subtracted from the data. The most remarkable features of Fig. 2b are the two domains of relatively strong responses in the central area, one centered at about X/R=0.1, Z/R=0.5 and the other at about X/R=0.35, Z/R=0.9. The phasors in these two domains differ in phase by about 180 deg, and therefore it is reasonable to identify them as being associated with a source that may be modeled as a current dipole lying under the center of the pattern. Studies with left and right visual field stimulation show that response amplitudes are little changed at positions anterior to X/R = 0.4, which is direct evidence that the source of the central field has a different

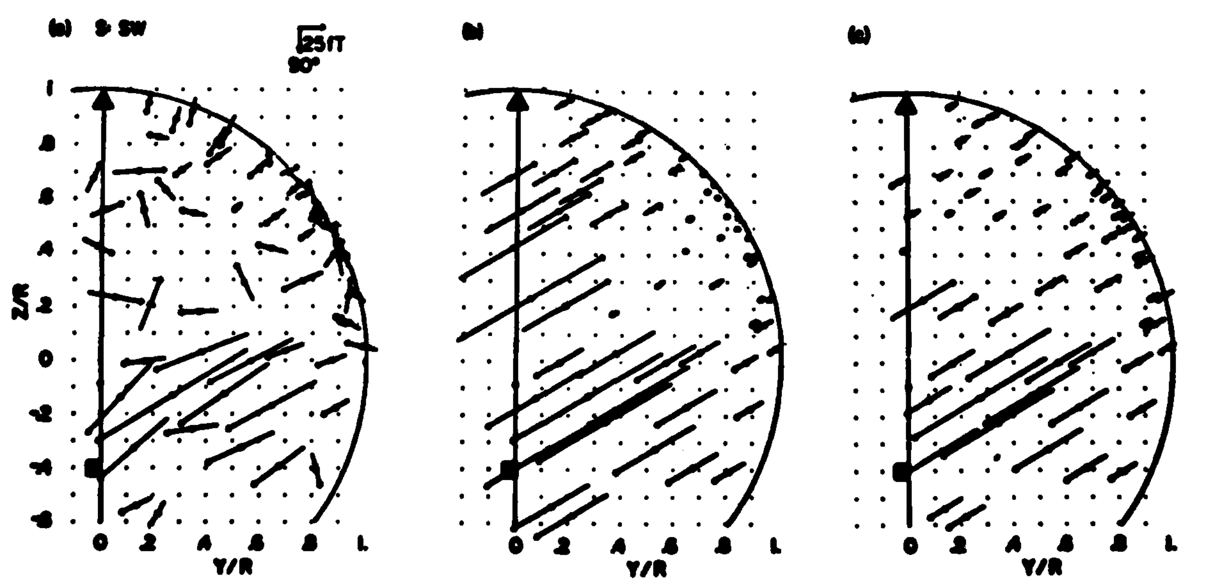

Fig. 1. (a) Observed responses over the occipital region (vertex is designated by a triangle and the inion by a square); (b) calculated contributions from RO source; (c) calculated contributions from both RO and LO sources.

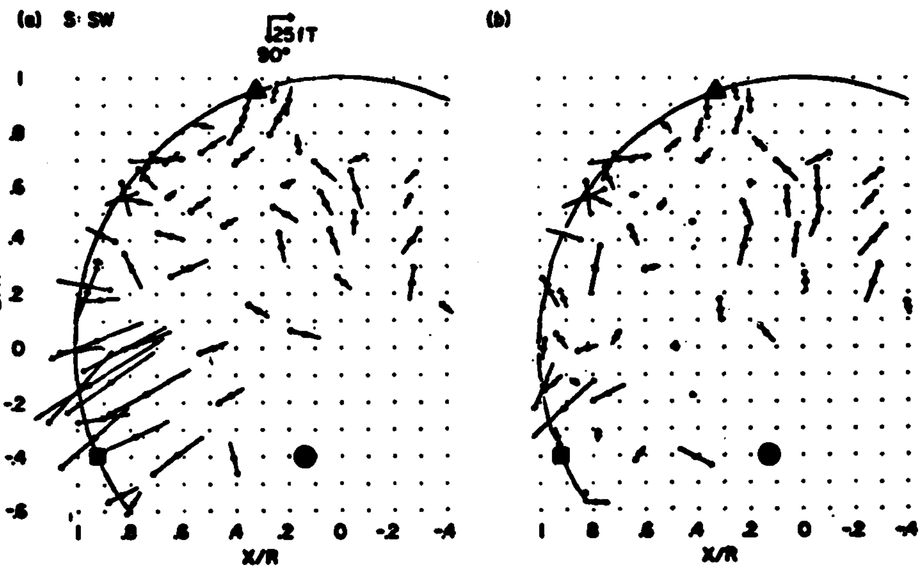

Fig. 2. (a) Observed responses over the right hemisphere (ear canal is designated by a circle); (b) observed responses with calculated contributions of RO and LO sources subtracted.

functional property than that exhibited by RO and LO. The medial temporal area of the macaque monkey also contains representations of ipsilateral and contralateral hemifields as does this one.

Figure 3a displays a dipolar field pattern that reproduces the essential features of the observations in Fig. 2b. When this pattern is subtracted from the phasers in Fig. 2b, what results is shown in Fig. 3b. The fit appears reasonable, aside from exceptional points at about X/R=-0.06, Z/R=0.66 and X/R=0.06, Z/R=0.7 which also display deviant phases in the original data of Fig. 2a. This right central (RC) source of the dipole pattern is characterized by the parameters in Table 1. We can relate the location of this source to the Rolandic fissure, which is well-established for this subject by sensorimotor studies (Okada et al., 1982).

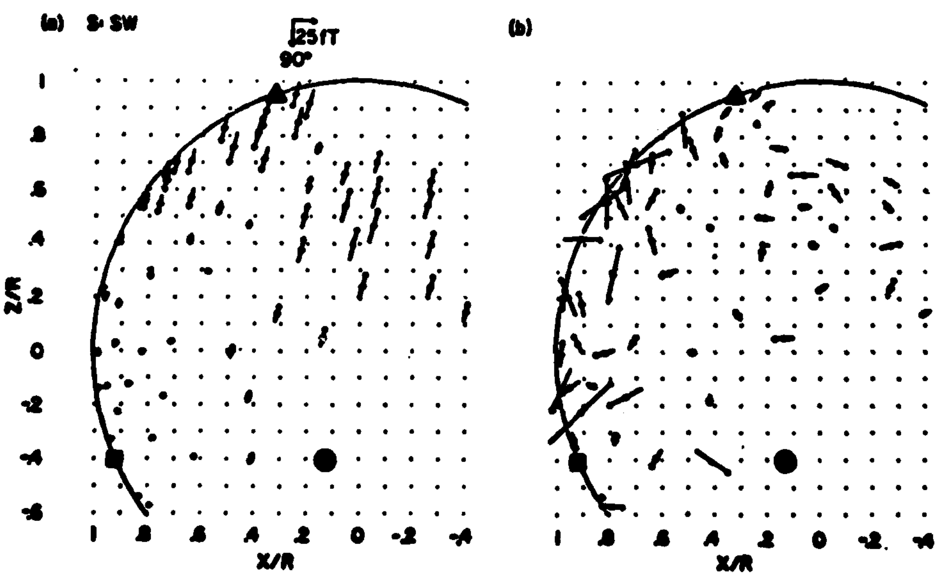

Fig. 3. (a) Calculated contributions of RC source; (b) observed responses with the contributions of RO, LO, and RC sources subtracted.

Table 1 Parameters for Model Dipole Sources (Subject: SW)

Source	θ (deg)	ϕ (deg)	Ψ (deg)	d (cm)	Q (nA-m)	Phase Lag (deg)
Right Occipital	90	6	125	2.0	6.0	150
Left Occipital	85	-15	260	2.0	6.0	150
Right Central	45	75	135	3.2	2.2	285

Motor activity associated with voluntary ballastic flexure of the left index finger is observed at about X/R=0.4, Z/R=0.8, a position 3 mm posterior to the Rolandic fissure as prescribed by Gray (1977). The position of RC is 2 cm lower along this fissure, and the orientation of its dipole is exactly perpendicular to the fissure.

DISCUSSION

Observations over the central area clearly reveal a magnetic response to this visual stimulus. This is in addition to the response over the occipital area, whose sources can be modeled by two approximately opposing current dipoles, representing the activity of the primary visual cortex along opposite sides of the longitudinal fissure. The fields over the central area may be ascribed to a current dipole lying deep within the Rolandic fissure near the eye area. One hypothesis explaining this activity could be that it is associated with motor activity related to eye movements in tracking the velocity modulation of the grating. We argue that this is unlikely, since the eye is incapable of tracking oscillations as rapid as 7 Hz. More likely, this activity is in response to signals ultimately originating in the visual cortex that are provided to the eye motor area for comparison purposes (c.f. von Holst and Mittelstaadt, 1950). This conjecture has some support in the preliminary observations in PL that there is a consistent increase in apparent latency on going from the occipital to central field patterns, and this suggests a causal relationship. Thus it appears that there is sequential activity, beginning in the occipital area and shifting to the central.

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